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XI. *On the Development and Homologies of the Carapace and Plastron of the Chelonian Reptiles.* *By Professor* OWEN, *F.R.S. &c.*

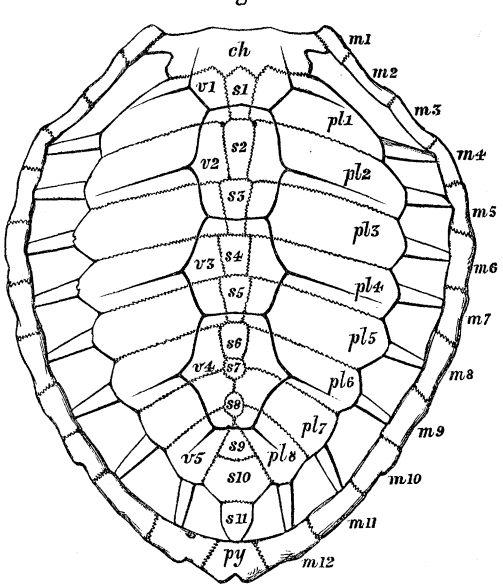
Received November 16, 1848,—Read January 18, 1849.

THOSE animals to which, in the manifold modifications of the organic framework, a portable dwelling or place of refuge has been given, in compensation of inferior powers of locomotion or other means of escape or defence, have always attracted especial attention; and of them the most remarkable, both for the complex construction of their abode as well as for their comparatively high organization, are the reptiles of the Chelonian order. The expanded thoracic-abdominal case, into which, in most Chelonians, the head, the tail and the four extremities can be withdrawn, and in some of the species, be there shut up by moveable doors closely fitting both the anterior and posterior apertures, as *e. g.* in the Box-tortoises (*Cinosternon, Cistudo*), has been the subject of many and excellent investigations; and not the least interesting result has been the discovery, that this seemingly special and anomalous superaddition to the ordinary vertebrate structure is due, in a great degree, to the modification of form and size, and, in a less degree, to a change of relative position, of ordinary elements of the vertebrate skeleton.

To ascertain the precise nature and extent of these modifications, in other words, to determine the homologies of the bony framework of the case in question, is the aim of the present communication.

The natural dwelling-chamber of the *Chelonia* consists chiefly, and in the marine species (*Chelone*) and mud-turtles (*Trionyx*) solely, of the floor and the roof: side-walls of variable extent are added in the freshwater species (*Emydians*) and land-tortoises (*Testudinians*). The whole consists chiefly of osseous 'plates' with superincumbent horny plates or 'scutes,' except in the soft or mud-tortoises (*Trionyx* and *Sphargis*), in which these latter are wanting. It is requisite briefly to allude to the well-known composition of the osseous framework of this chamber in order to define the terms by which certain parts will be adverted to in the course of the paper.

Fig. 1.



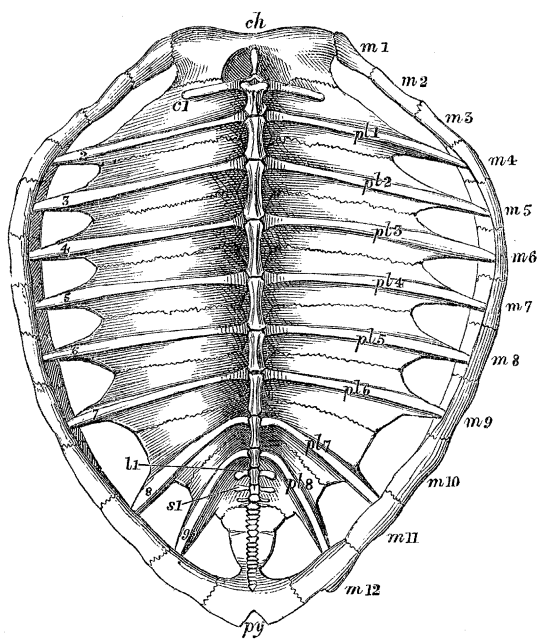
Carapace of the Loggerhead Turtle (*Chelone caouanna*).

The roof or 'carapace' (fig. 1) consists of a

'median' series of symmetrical plates (*ch*, s_1 to s_{11}), and of two 'lateral' series forming a pair (pl_1 to pl_8), the whole being surrounded by a circle of 'marginal' pieces (m_1 to *py*), completed anteriorly by *ch*, the first of the median series. Of the median series eight (s_1 to s_8) are attached to the spines of eight subjacent vertebræ: the lateral or parial plates (pl_1 to pl_8) are attached to, and more or less blended with, the ribs of the same vertebræ, and the ends of these ribs usually articulate by gomphosis with a corresponding number of the marginal pieces, of which, however, there may be from twenty-four to twenty-six, including the two median and symmetrical ones (*ch* and *py*). That these marginal pieces are the least essential parts of the carapace is shown not only by their inconstant number, but by their partial or total absence in some of the soft-turtles (*Gymnopus*, *Sphargis*).

In the present communication the median pieces (s_1—s_{11}) are called the 'neural' plates; the lateral pieces (pl_1—pl_8) the 'costal' plates: the term 'marginal' is restricted to those peripheral pieces which form pairs (m_1 to m_{12}); the anterior symmetrical piece (*ch*), constant in all *Chelonia*, is called the 'nuchal' plate; the posterior symmetrical piece (*py*), which is wanting in all the *Trionycidæ*, is the 'pygal' plate. I enumerate the neural plates in the order in which they are numbered by Bojanus in the Tab. III. and IV. of his great work*. The neural arch connate with the first neural plate (s_1) is supported partly by the centrum of the vertebra to which the first pair of free ribs (fig. 2, c_1) is articulated, and which, therefore, is reckoned as the first dorsal vertebra: these ribs are small and slender, attached at both their extremities, the outer end abutting against the under part of the first pair of costal plates, which they help to sustain. The second to the ninth dorsal vertebræ inclusive, being those which are more immediately connected with the neural and costal plates, may be called 'vertebræ of the carapace:' their characters, though not less artificial than those which distinguish the 'dorsal' or 'lumbar' vertebræ of other reptiles, are much more marked and constant. The eighth vertebra of the carapace is succeeded by a vertebra, which in some species (*e. g. Chelone caouanna*, fig. 2, l_1) supports a pair of short ribs, in others (*Trionyx*) none, and which is therefore reckoned a 'lumbar' vertebra; this is followed by two other vertebræ, with short and thickened ribs, abutting against the iliac bones and representing the 'sacrum' (fig. 2, s_1): as these three vertebræ are not immediately united with the ninth, tenth

Fig. 2.



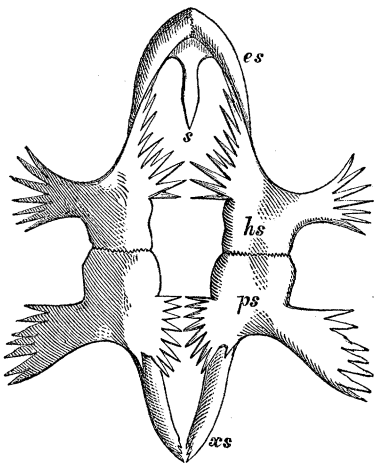
Inner view of the carapace of the Loggerhead Turtle (*Chelone caouanna*).

* Anatomia Testudinis Europææ. Fol. 1819–1821.

and eleventh 'neural plates,' they have less claim than the first dorsal vertebra to be regarded as entering into the composition of the carapace.

The 'plastron' (fig. 3) or floor of the thoracic-abdominal chamber consists in all *Chelonia* of nine pieces, for which the terms proposed by Geoffroy St. Hilaire may be retained, if used in an arbitrary sense and without implying assent to the hypothesis that first suggested them. The median and symmetrical piece of the plastron (fig. 3) is the 'entosternal' (*s*), the four pairs, counted from before backwards, are respectively, the 'episternals' (*es*), 'hyosternals' (*hs*), 'hyposternals' (*ps*), and 'xiphisternals' (*xs*).

Fig. 3.



Plastron of *Chelone caouanna*.

With regard to the ideas that have been entertained as to the homologies of the above-defined osseous pieces, it would be a parade of names without adequate gain to the discussion, to go further back than the first edition of the "Leçons d'Anatomie Comparée" (1799), in which Cuvier refers the chief part of the carapace, viz. the 'costal plates,' to eight pairs of dilated ribs*: the neural plates he describes as corresponding in number with the vertebræ of which they form part†: the marginal pieces and the parts ("plusieurs os") of the plastron are described arbitrarily and left undetermined.

Geoffroy St. Hilaire, entering into the question of their homologies in his memoir on the genus *Trionyx*, published in the year 1809, and adopting the Cuvierian idea that the carapace consisted of a development of dorsal vertebræ and vertebral ribs, argues that the plastron is a greatly expanded sternum, and that the marginal pieces are the cartilages of the ribs ossified, or 'sternal ribs' ("côtes sternales‡").

In the collection of memoirs forming the first edition of the 'Ossemens Fossiles,' Cuvier merely cites the opinion of Geoffroy, "Ces pièces que M. Geoffroy compare à la partie sternale ou cartilagineuse de nos côtes manquent aux *tortues molles*,"

* "La carapace des Tortues est formée par les dilatations de huit côtes ou batons osseux qui prennent naissance sur les unions des vertèbres et se terminent à un rebord que entourent toute la carapace." Tom. i. p. 211.

† "On remarque en dessus, le long de la partie moyenne, une rangée de petites plaques osseuses presque carrées, unies intimement entre elles par synarthrose, qui sont en même nombre que les vertèbres dont elles font partie." Ib. p. 211.

‡ "La différence dans le nombre des pièces du plastron et du sternum des oiseaux pouroit faire croire qu'il seroit entré dans le plastron des tortues des pièces étrangères à la composition d'un sternum, comme des côtes sternales; idée d'autant plus naturelle à admettre, que les parties latérales du plastron sont terminées par un certain nombre de digitations; cependant il n'en est rien. Les analogues des côtes sternales ne manquent point dans les tortues; elles existent dans ces pièces articulées dont j'ai parlé plus haut, et se voient à la suite des côtes vertébrales ou elles forment le bord des carapaces. Le plastron, ou le sternum des tortues s'attache sur ces côtes ou pièces sternales, en sorte qu'il ne manque rien d'essentiel dans le thorax des ces animaux."—*Annales du Muséum*, xiv. p. 7 (1809).

&c. (see the concluding memoir of tom. iv. 1812, p. 2). In the second edition of the 'Ossemens Fossiles' (tom. v. pt. 2. 1824), CUVIER, after remarking "that the marginal pieces do not correspond exactly to the vertebral ribs; that the first of the dilated ribs forming the carapace joins the third of the marginal pieces; and that the tenth does not receive any rib," observes, in reference to the latter expression, "ne reçoit aucune côte.... Ce ne pourroit donc être aussi que sous un point de vue philosophique que l'on regarderoit les pièces marginales comme réprésentant les cartilages ou parties sternales des côtes. Toutefois, comme il y en a onze, ce qui est précisément le nombre des vertèbres dorsales et lombaires, c'est un motif pour adopter ce point de vue. Les deux premières et les deux dernières servaient, comme on l'a dit en d'autres occasions, des côtes sternales auxquelles leurs côtes vertébrales manqueroient," p. 200. In the posthumous edition of the 'Leçons d'Anatomie Comparée,' CUVIER gives only grounds for rejecting, not any for adopting, the views of GEOFFROY, in regard to the marginal pieces, and observes, "On a considéré ces pièces comme analogues aux portions sternales des côtes: il faut avouer au moins qu'elles ne leur répondent pas pour le nombre, et que dans les trionyx sur-tout, elles ne leur correspondent point pour la position. C'est à la troisième ou à la quatrième que commence leur engrenage avec les deux pièces moyennes du sternum; il finit à la huitième, mais dans les tortues de mer cette union n'a pas lieu." Tom. i. 1835.

BOJANUS, who has given the most complete and masterly analysis of the emydian modification of the carapace and plastron, calls the neural plates 'processus spinosi vertebrarum dorsi,' the costal plates 'costæ,' and the bones of the plastron 'sternum:' he offers no homology of the 'marginal' plates, but retains for them the absolute names of 'ossa marginalia*.'

The eminent physiologists and comparative anatomists of our own country have not, however, partaken of this reserve of the great French master of the science, or of the celebrated German monographer, towards the Geoffroyan hypothesis of the marginal pieces. Dr. ROGET, in his 'Bridgewater Treatise,' after a brief but clear summary of the general structure and uses of the carapace and plastron, says, "We find, however, on a more attentive examination, that all the bones composing the skeleton in other vertebrated animals exist also in the Tortoise; and that the bony case which envelopes all the other parts is really formed by an extension of the spinous processes of the vertebræ and ribs on the one side, and of the usual pieces which compose the sternum on the other." Vol. i. 1834, p. 464. The learned Professors of Comparative Anatomy in University College and King's College, London, have in like manner adopted absolutely the determinations of GEOFFROY ST. HILAIRE, although the former admits that†, "Looking at the singular exterior of these tortoises, shielded in a solid case like a molluscous animal in its shell, we should scarcely expect to find that this dense osseous covering enveloping the whole body consists of the same

* *Op. cit.* p. 12.

† Lancet, February 8, 1834. See also Prof. GRANT's 'Outlines of Comparative Anatomy,' 8vo, 1835, p. 82.

bones which compose the human skeleton:" and I must frankly avow that my expectation of such a discovery was so small as to beget neither surprise nor disappointment when the result of my researches into the development of the parts demonstrated on how superficial a view it had been entertained.

Professor Rymer Jones, in his beautifully illustrated 'General Outline of the Animal Kingdom,' adopting Cuvier's determination of the 'carapace' and Geoffroy's of the 'plastron,' observes, "The margin of the dorsal ribs is further enlarged by a third set of flat bones, apparently representing the sternal ribs of the Crocodile." 8vo, 1841, p. 553. In his article Reptilia, however, in Todd's Cyclopædia, Part 32, August, 1848,—the latest opinion on the subject which has been published,—the Professor affirms, "these marginal plates cannot be otherwise regarded than as the representatives of the sternal ribs of the Crocodiles and other Saurians." P. 266.

The German authors of standard works on comparative anatomy, with the exception of Meckel*, have manifested no such general acquiescence in the views of Geoffroy St. Hilaire, as that which characterises those of our countrymen above-cited. Carus, for example, originally regarded the immoveable 'costal plates' of the carapace as much-developed transverse processes, and the thorax of the Tortoise to be "only a more perfect development of the ribless and imperfect thorax of the Frog†;"—a view, however, in which his able English translator does not concur‡; and which Carus himself abandons in the second edition of his work. He there states that the remarkable and anomalous skeleton of the trunk of the *Chelonia* may be explained by recognising how certain plates belonging primitively to the dermal skeleton are applied or adapted to the vertebræ, the ribs and the sternum§: the idea, however, is neither explained in detail nor supported by any fact of development, but is rather obscured by such fancies, as that the bodies of the vertebræ of the carapace are not formed, as usual, on the under side, but on the upper side of the vertebral column in the place of the spinous processes, which Carus affirms not to exist‖.

Dr. Peters¶ adopts the view that the carapace includes dermal pieces besides the vertebræ and ribs; and that the plastron consists of a subdivided sternum enlarged by combination with ossified parts of the integument.

Professor Wagner has given us an opportunity of judging of the sense in which he

* System der Vergleichenden Anatomie, Zweiter Theil, Erst. Abth. pp. 407, 408.

† Introduction to Comparative Anatomy, by Gore, 8vo, 1827, p. 147.

‡ See the note at the same page, where the Geoffroyian interpretation is given, as more correct.

§ "Die Bildung des Rumpfskelett's nur dadurch erklärlich wird, das man einsehen lernt, wie durch Anbildung eigner, ursprünglich dem Hautskelet angehöriger Platten an Rückgrath, Rippen und Brustbein, die auf den ersten blick so sonderbar abweichende Bildung des Rücken- und Bauchschildes zu Stande kommt." Lehrbuch der Vergleich. Anatomie, 8vo. Bd. i. p. 164.

‖ "Am Rückenschilde das völlige Verwachsen der Wirbel, deren körper hier nicht wie gewöhnlich an der untern, sondern an der obern Wirbelseite, statt natürlich ganz fehlenden, und durch die darauf gelegten Knochenplatten des Hautskelets ersetzlen Dornfortsätze ausgebildet sind." Ib. p. 165.

¶ Observationes ad Anatomiam Cheloniorum, 1838.

understood Carus's idea, by the figure of the skeleton of a young Sea-turtle (*Chelone caouanna*), which he explains in his excellent 'Icones Zootomicæ,' fol. 1841*, Tab. XIV. fig. 12; where *a* are the ribs, *b* the vertebral bodies, *c* the neural arches (bogentheile), *d* the neural spines, and *e e* the median row of dermal bones ('mittlere Reihe der Hautknochen,' p. 17). Now these latter, in the figure, are six in number, extending from one end of the carapace to the other, whilst the subjacent neural spines agree in number with the vertebræ, of which there are twelve between the scapula and ilium. It is plain, therefore, that the horny 'vertebral scutes,' as they are called in Erpetology, are here the parts supposed to represent the dermo-skeleton, and that the bony 'neural plates' are regarded as the spinous processes, agreeably with the Cuvierian view.

Prof. Rathke† has recently propounded another modification of the combined dermo- and endo-skeletal hypothesis of Carus. Finding that there were no osseous plates developed independently in the corium and afterwards coalescing with the neural spines and ribs, as Carus and Wagner describe, he concludes that the carapace of the *Chelonia* is composed exclusively of endo-skeletal elements, but that the plastron as exclusively consists of exo-skeletal parts or dermal bones, in which category also he places the 'marginal pieces,' sufficiently proved by the *Trionyx* and *Sphargis* to be not essential to the composition of the carapace.

The special deductions by Rathke will be compared, in the sequel, with my own observations on the development of the carapace in the *Chelonia*; but it will be obvious, from the conflicting opinions on the nature and homologies of the chelonian skeleton, published within the last ten or fifteen years, that the question is far from having been satisfactorily settled; and that no one can be regarded as giving the requisite description of the carapace and plastron who merely adopts the determinations of Geoffroy, or Carus or Rathke, without first testing them by an appeal to nature, and assigning the grounds of his acceptance, rejection or modification of such determinations.

Commencing by the way of a comparison of the skeletons of fully-developed Vertebrata, and assuming for the purpose of such comparison that the thoracic-abdominal case is a modification of parts of the endo-skeleton, as Cuvier, Geoffroy and Meckel believed, I propose in the first place to test the homologies which have been generally accepted in this country, and of which, as regards the 'marginal plates,' so positive an opinion has been recently published.

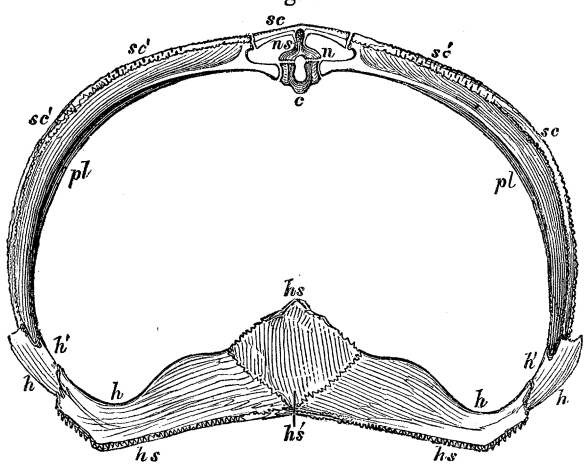
Geoffroy St. Hilaire was guided, as is well known, to his conclusions by the

* "Hier ist das skelet einer jungen Seeschildkröte (fig. xii) zu vergleichen, wo man sieht, dass Wirbelsäule, Rippen und Brustbein in ihrer ursprunglichen Anlage von dem eigentlichen Rücken- und Brüstschild ganz getrennt sind; das dieses eigentlich aus isolirten Verknöcherungen in der Haut entsteht, welche erst später mit Knochenskelet verwachsen." p. xii.

† Sur le dévelopment des Cheloniens. Annales des Sciences, Mars, 1846; and Ueber die Entwickelung der Schildkröten. 4to. 1848, p. 122.

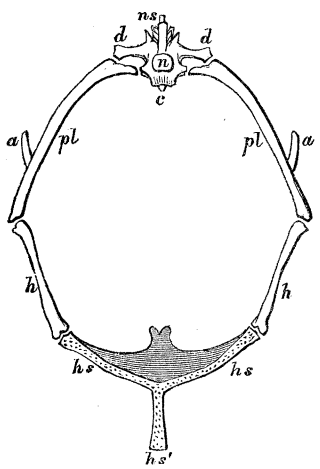
analogy of the thorax of the Bird: but they are not elucidated by any special descriptions or figures. They will be, perhaps, best understood by comparing the subjoined view of a segment of the thoracic-abdominal case of the Tortoise (fig. 4) with the corresponding view of the homologous segment in the Bird (fig. 5); in both of which *c* is the vertebral body or 'centrum,' *n* the neural arch, *ns* the neural spine, *pl* is the vertebral rib (pleurapophysis), *h* (the outer letter in fig. 4) is the ossified sternal rib (hæmapophysis), and *hs* the hæmal spine or 'sternum.' In this comparison it is supposed that the primitive median division of the sternum is retained in the cold-blooded reptile, and that the keel, or 'entosternal' piece (*hs'*), continues distinct, but is developed in breadth instead of depth. No one, however, has been able to adduce any example from the class of birds in which the lateral moieties of the broad sternum are developed each from four distinct centres, answering to the four lateral or parial pieces in the plastron of the *Chelonia* (*es*, *hs*, *ps* and *xs*, fig. 3).

Fig. 4.



Thoracic segment, Tortoise.

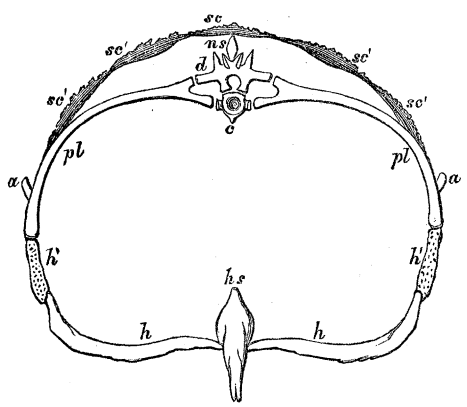
Fig. 5.



Thoracic segment, Bird.

The homologies of the carapace and plastron, regarded as developments of the endo-skeleton, appear, hitherto, not to have been elucidated by any other comparison, save that by CARUS with the thorax of the Frog. Yet the chelonians have nearer affinities to the crocodiles than to either birds or batrachians; and a comparison of the thoracic-abdominal part of the skeleton of a crocodile appears to give correspondingly closer illustrations of the nature of the peculiarities of that in the Tortoise. In the subjoined view of the segment of the thorax of a crocodile (fig. 6), it will be observed

Fig. 6.



Thoracic segment, Crocodile.

that a distinct piece *h'* is interposed between the pleurapophysis (*pl*) and hæmapophysis (*h*), and it is less completely ossified than either of those elements. The sternum *hs* is a single symmetrical rhomboidal plate, of which a narrow median portion only is completely ossified. With the endo-skeletal segment is combined, in the figure, parts of the corresponding ossified segment of the exo-skeleton, which parts are covered, like the expanded parts of the carapace of the *Chelonia*, by thick cuticular scutes. According to this analogy, *c* being the centrum and *ns* the neural arch and spine, *sc* answers to the detached dermal bony plate *sc* in fig. 4. The head, neck and continuous slender part of the rib (*pl*, fig. 6) answers to the pleurapophysis (*pl*) in fig. 4, and the expanded plate (*sc'*, fig. 4) answers to the lateral bony dermal plates (*sc'*, *sc'*, fig. 6): the marginal plate *h*, *h'*, fig. 4, occupies the place of the intercalated costal piece *h'*, fig. 6: the hyosternal *h*, *hs*, fig. 4, answers to the hæmapophysis or ossified cartilage of the rib (*h*, fig. 6), the other parial pieces also being expanded hæmapophyses; and the entosternal *hs* (fig. 4) alone represents the simple sternum *hs* in the Crocodile: in brief, the figures within the segment fig. 4, indicate the homologies according to the Crocodile (fig. 6), those without or below the segment (fig. 4) indicate the homologies according to the Bird, fig. 5.

In this comparison it will be seen that the mesial end of the costal plate (*sc'*, fig. 4), which quits the rib to articulate with the vertebral plate (*sc*) in the Tortoise, is not the homologue of the tubercle of the rib which articulates with the diapophysis *d*, fig. 6, in the Crocodile: the true endo-skeletal pleurapophyses, or vertebral ribs, of the Chelonians I regard as being simple, and articulated by a head only to the central part of the vertebra, as in other Reptilia which have but one ventricle of the heart. They are almost straight, and so far resemble the free ribs (pleurapophyses), which project from a few of the dorsal vertebræ in the *Pipa* or Surinam Toad.

Were the large and complex abdominal hæmapophyses of the Plesiosaur (fig. 7, *h*) to coalesce on each side, they would form two lateral masses with their extremities projecting outwards and inwards, like the teeth of the hyosternals (*hs*) and hyposternals (*ps*) in the plastron of the *Turtles* and *Trionyces* (figg. 3 and 8).

In offering the comparison of the thoracic-abdominal segment of the Crocodile with that of the Chelonian to the consideration of Comparative Anatomists, my object has been rather to show that the subject admits of more than one view, and requires further investigation, than to substitute merely by such comparison a different homological hypothesis from that which has hitherto prevailed in this country; being conscious that without the illustrations of which such hypothesis may be susceptible, it would be of as little real avail in attaining to a true knowledge of the vertebrate organization of the *Chelonia* as the similarly unconfirmed view of Geoffroy St. Hilaire must be considered to be. The guide to our choice of either of these, or of any other view that has been offered of the nature and signification of the thoracic-abdominal case of the *Chelonia*, must be the light afforded by a true perception and explanation of the phenomena of its development.

The youngest Chelonian which I have had the opportunity of examining has been the embryo of the common Turtle (*Chelone Mydas*), not quite an inch in length (Pl. XIII. figs. 1, 2, 3). At this period the broadest part of the animal is the head, across the large prominent eye-balls. The neck is shorter than the head, the carapace is a long narrow ellipsoid, more convex than in the adult, defined by a feebly-indicated, thickened border: the region of the plastron (fig. 3) is flatter, perforated by the large vitelline duct and vessels (*u*). The scapular arch (fig. 2 *a*, 51, 52) divides the base of the neck from the fore-part of the carapace and plastron, and the anterior and posterior limbs present the simple form of undivided paddles, which they afterwards retain in this and other marine species. Although the ribs (fig. 1 *a*, d_1 to l_{10}) are visible through the integument of the back, and the slender entosternum (fig. 3 *a*, *s*) and two transverse linear rudiments of the plastron (*hs* and *ps*), on each side, are more obscurely seen beneath the integument of the abdomen, yet the corium covering these parts is thicker, and its texture denser than in the embryo of the lizard or that of the fowl of corresponding size and development; the general resemblance in the form of the body being very close at this period, to the bird, by reason of the normal proportions of the trunk and the shortness of the tail. The most advanced parts of the osseous system are plainly those which belong to the endo-skeleton, and which at this period deviate comparatively little from the normal type. As my present object relates to the thoracic-abdominal case, I shall confine my remarks chiefly to that part of the skeleton.

Ossific matter has begun to be deposited in the cartilaginous foundations of the neurapophyses (figs. n_1—n_{10}, 1 *a*, 2 *a*), and of the pleurapophyses (d_1—l_{10}), but not in the neural spines or the centrums.

Ten pairs of pleurapophyses (dorsal or vertebral ribs) have been established, much more nearly equal at the present than at a subsequent period; the first (d_1) and the two last (d_9 and l_{10}) being the shortest: all of them are simple, slender, cylindrical, slightly bent towards the ventral surface, terminating freely near the thickened border of the dermal basis of the carapace. The scapulæ (*ib.* 51) closely resemble the other pleurapophyses: it is impossible to mistake their general homology as the same elements of the vertebral segment: they are equally simple and cylindrical, and their ossification has made the same progress: but their position is more nearly vertical, with the upper end abutting against the fore-part of the first thoracic rib ($d1$), and the lower end bent inwards towards the entosternum (*s*); the position is very similar to that which the scapula presents in the correspondingly developed embryo of the bird, in which, by a subsequent movement of backward rotation, the slender rib-like scapula comes to overlap the anterior thoracic ribs: but the primitive vertical position—the more normal position in relation to the archetypal skeleton—is retained throughout life in the *Chelonia* as in the *Monotremata*. In the region of the plastron the entosternum is represented by a slender median cartilage, pointed behind (fig. 3 *a*, *s*) the hyosternals (*hs*) by a pair of transverse cartilages, commencing near the

median line anterior to the umbilical aperture (*u*), and arching outwards, forwards, and slightly upwards to near the ends of the third pair of ribs: the hyposternals (*p s*) are represented by a similar transverse pair of slender cartilages, with a tendency to bifurcate at their extremities. The cartilaginous foundations of the episternals and xiphisternals have a not very definite linear form: the coracoids (fig. 1 *a*, 52) are more plainly distinguishable; I at first mistook them for the episternals. The rudimental hyosternals and hyposternals at this period repeat the characters of the sternal or abdominal ribs (hæmapophyses) in the Crocodile; the entosternum represents the thoracic sternum of the Crocodile.

The thick and somewhat dense corium of the carapace, covering the rudiments of the neural arches and pleurapophyses, when examined under a power of 300 linear diameters, does not present exclusively the fine filamentous interlaced structure of cellular tissue in progress of condensation into derm, as in the embryo bird; but includes oblong nucleated cells, like those of cartilage, which along the middle line of the back are arranged in groups of linear series radiating from a centre corresponding with the point of convergence of each pair of neurapophyses, and connected with the extremities of those cartilages by a mass of cartilage-corpuscles holding the place of the neural spines.

The cartilage-corpuscles in the firm semiopake part of the corium covering the ribs, show traces of linear arrangement at right angles to the ribs, or in the axis of the carapace; especially near the proximal ends of the middle ribs. The thickened border which defines the carapace is formed almost entirely of oblong nucleated cartilage-corpuscles, pretty closely aggregated and without observable definite arrangement. The stratum of cartilage-corpuscles in the substance of the corium of the plastron is thinner than that of the carapace: something like a linear radiated arrangement of these may be discerned at the parts corresponding to near the mesial ends of the hyosternals and hyposternals; but they are for the most part irregularly and more thinly scattered in the fibrous tissue than on the carapace.

Homologically I conceive that this basis for future ossification, being situated in the substance of the skin, must be held to be the groundwork of a dermal skeleton; and that, whether ossification extends into such basis from the subjacent ossifying parts of the endo-skeleton, or whether it commences independently in the dermal cartilage, and afterwards unites with the deeper-seated bones, does not affect such homological relation: in other words, that a dermal bony scute, whether it be connate or become confluent* with a part of the endo-skeleton, is still essentially a dermal bone.

But although, with regard to most of the superadditions to the endo-skeletal basis of the carapace, I have not been able to distinguish a period of the development of an independent centre of ossification, yet the superadded parts, ossified from pre-

* I use the terms 'connate' and 'confluent' in the sense defined in my work on the 'Archetype of the Vertebrate Skeleton,' 8vo, p. 49.

existing subjacent vertebral elements, long retain a very peculiar and distinct character of osseous texture, well-displayed in the development of the carapace and plastron of the land-Tortoises, which I next proceed to describe.

Fig. 4 gives an outside view of the incipient carapace of a very young *Testudo indica*: fig. 5 shows an inside view of the same carapace, and figs. 6 and 7 similar views of the plastron of the same.

The carapace is not quite three inches in length. On removing, after maceration, the well-developed epidermal scutella, the following ossified parts were seen:—the nuchal (*ch*), the pygal (*py*), and ten intervening neural plates ($s\,1$ to $s\,10$); mostly of a subquadrate form, but of irregular size, and with rounded angles and ill-defined outlines; the tenth plate ($s\,10$) being insulated between the ninth ($s\,9$) and the pygal plate (*py*). On each side of the middle row of neural plates is a series of eight similarly-sized, triangular or rhomboidal plates (fig. 4, $pl\,1$—$pl\,8$), each of them marked on their outer surface with a triradiate linear impression formed by the junction of two costal scutella with one vertebral scutellum, or of one vertebral with two costal scutella; excepting the penultimate or seventh plate ($pl\,7$). Around the border of the carapace are eleven pairs of marginal plates ($m\,1$—$m\,11$), exclusive of the nuchal (*ch*) and pygal (*py*) plates. The wide interval between the marginal and the incipient costal plates is occupied by the corium and its stratum of cartilaginous cells, supported by the eight pairs of ribs of the carapace (fig. 5, $d\,2$—$d\,9$), by the first pair of short dorsal ribs ($d\,1$), by the pair of shorter lumbar ribs, and by the rib-like upper and outer extremities of the hyosternals (*hs*) and hyposternals (*ps*), which ascend beyond the marginal plates. The extremities of the ribs do not as yet join the marginal plates. The nuchal plate, the ninth and tenth neural plates, the pygal plate, and all the marginal plates are independent osseous developments in the substance of the derm: the other neural plates ($s\,1$—$s\,8$) are connate with the neural spines of the second to the ninth dorsal vertebræ inclusive, and the costal plates are similarly connate with the upper surface of the ribs of the same vertebræ at varying distances from their proximal ends. The first, second, fourth, sixth and eighth ribs of the carapace are continued from beneath the outer angles or apices of the corresponding costal plates ($pl\,1$, $pl\,2$, $pl\,4$, $pl\,6$, $pl\,8$), but the third, fifth and seventh ribs of the carapace are continued from beneath the middle of that side of the corresponding triangular costal plate which seems to form its base.

The neural plates, the costal plates, and the marginal plates, whether attached to vertebral elements or detached, are lodged in the substance of the derm, and form a stratum of bones superficial to the ossified parts of the endo-skeleton. A strong argument for regarding the costal plates as dermal ossifications rather than processes or continuations of the endo-skeletal elements, to which they are attached, may be drawn not only from the place of development of their cartilaginous basis or bed, but also from the period of their ossification; and their relative position to the ribs with which they are connate.

In the embryo *Testudo indica* the uniformly slender pleurapophyses (*d* 1—*d* 9, fig. 5) are ossified nearly throughout their whole length before the ossification of the costal plates, usually regarded as their expanded tubercles, commences: and the beginning of the superadded bone* is not at the same point in each rib, as might have been expected if it were the exogenous process called 'tubercle' of the rib. The costal plates are situated in the young *Testudo indica* (Plate XIII. figs. 4 and 5, *pl* 1—8) alternately nearer to and farther from the head of the rib; and their presence seems to be determined rather by the angle of union of the superincumbent vertebral scutella with the lateral or costal scutella, than by the necessity for additional strength in the articulation of the ribs with the spine. Ossification commences at the point from which the three impressions radiate, and as this point is nearer the median line at the median apex of the costal scutellum than at the lateral apex of the vertebral scutellum, the resulting plates of bone are alternately further from or nearer to the middle line; and the first, third and fifth costal plates have advanced along the proximal end of the rib so as to join the neural plates, whilst the second, fourth and sixth costal plates leave a portion of the proximal end of the rib uncovered and crossing the space between the incipient costal plate and the neural plate. In regarding these incipient ossifications, extending into the substance of the corium and receiving the impressions of the epidermal scutes as the developed 'tubercle' of the ribs, as RATHKE has endeavoured to illustrate in Tab. III. figs. 11 (Tortoise), 12, and 13 (Chick) of his elaborate Monograph†, we are compelled to suppose that each successive rib in the Tortoise has a different position of its tubercle, which is alternately nearer and farther from the head, and that the neck of each successive rib is alternately long and short, which is contrary to all analogy furnished by those cold-blooded or warm-blooded *Vertebrata* that have unquestionably the exogenous process called 'tubercle' developed from the true neck of the rib.

When the partially ossified carapace of a young tortoise is dried, one cannot fail to be struck with the difference in the texture and external surface of the bones which unquestionably belong to the endo-skeletal vertebræ, and of those which, notwithstanding their connection with the neural spines and pleurapophyses, are developed in the fibrous substance of the corium. These nascent 'neural' and 'costal plates' of the carapace have a granular exterior and a coarse spongy texture, whilst the neural arches and pleurapophyses are compact, smooth, and with a polished external surface: the part of the pleurapophysis (Pl. XIII. fig. 5, *d* 2—*d* 9) which passes beneath and is attached to the under surface of the 'costal' plate (*pl* 1—*pl* 8), contrasts strongly with that superimposed dermal ossification.

The marginal plates (*m* 1—*m* 11)present the same rough, coarse, granular character as the neural and costal plates: they are in no way connected in their development

* This period, in its relation to the development of the neural arches and pleurapophyses, corresponds precisely with that at which the dermal plates of the Crocodile begin to be ossified.

† Ueber die Entwickelung der Schildkröten, 4to.

with the pleurapophyses, which do not yet reach them: their ossification has been governed by the presence of the marginal epidermal scutes, and, as in the case of the costal plates, by the points of junction of contiguous scutes; each marginal ossification is accordingly impressed by the lines indicating the junction of the marginal epidermal scutes with each other and, in the case of the middle ones, with the contiguous scutes of the plastron. The number of the marginal plates accords, moreover, with that of the marginal epidermal scutella, not with that of the ribs.

The plastron of the immature Tortoise (figs. 6 & 7) presents the same difference in the texture and surface of the endo-skeletal and exo-skeletal parts of the incipient bones as does the carapace: the triangular entosternal bone (*s*), the greater part of the episternals (*es*) and xiphisternals (*xs*), and a smaller proportion of the hyosternals (*hs*) and hyposternals (*ps*), are compact bone with a smooth shining free surface: the greater part of the broad hyosternal and hyposternal plates, the entire and even margins of which are encroaching on the central unossified space of the plastron, are subgranular, coarser and more opake than the slender endo-skeletal parts, which still retain much of the primitive rib-like form they presented in the fœtal *Chelone*, and are seen applied, as it were, to the inner (upper) surface of those dermal plates. The median extremities of the true endo-skeletal parts have begun to expand, and to shoot out the pointed rays of tooth-like processes which they retain in the *Trionyces* and the marine *Chelonia* (fig. 3). From the flattened and expanded inner and lower end of the hyosternal (fig. 7, *hs*) the main body of the bone arises and curves upwards, outwards and forwards, in the form of a long and slender rib, and applies itself to the inner and fore part of the first elongated pleurapophysis of the carapace, extending as far as the incipient dermo-costal plate; the rib-like part is represented detached from the rest of the hyosternal in fig. 5, *hs*. As the inner and lower toothed border of the endo-skeletal part of the hyosternal touches the outer border of the entosternal bone, the hæmal arch of the first segment of the thoracic-abdominal case (second vertebra of the back) is completed independently of the marginal pieces; and, in point of fact, the third and fourth marginal plates (fig. 8, *m*) are simply applied to the outer side of the hyosternal (*h*) where it bends upwards to join the first long pleurapophysis (*pl*) or rib of the carapace. The most obvious, and, I believe, the most natural explanation of this first complete segment of the thoracic-abdominal region of the young Tortoise, according to the typical vertebra, and the composition of the corresponding segment in the nearest allied *Vertebrata*, is—that the centrum (Pl. XIII. fig. 8, *c*), the neural arch (*ns*), and the pleurapophysis (*pl*), are the parts so indicated by the initial letters; that the hyosternals (*h*) are the hæmapophyses (sternal ribs or costal cartilages), and the entosternum (*hs*, *s*) is the 'hæmal spine' or sternum proper. The hyposternals in the young *Testudo* resemble the hyosternals, but are shorter; the slender rib-like portion which curves upwards and outwards applies itself to the back part of the extremity of the fifth rib of the carapace (fig. 5, *ps*), almost filling the interspace, for one-fourth of its length, between that rib and the next, and thus again forming the hæmal arch

of the segment without the intervention or aid of any of the marginal plates, the seventh of these being simply applied to the outside of the hyposternal, where its slender elongated extremity bends upwards to join the vertebral rib: and the only incomplete part of the arch is the unossified median space between the lower expanded and dentated ends of the hyposternals, between which the entosternal, or true sternal piece, does not extend backwards. So that the condition of this fifth segment of the thoracic-abdominal box, in the young Tortoise, repeats that of a posterior dorsal segment of a mammal or crocodile, in which the cartilages of the ribs, or abdominal ribs, do not reach the sternum; and the *Ornithorhynchus* offers a special resemblance to the Tortoise in the expansion of the semiossified hæmapophyses, or cartilages of its 'false ribs.' The xiphisternals, viewed in like manner as 'hæmapophyses', repeat the condition of those abdominal ones in the Crocodile and Plesiosaur which do not ascend so high as to join their pleurapophyses or vertebral ribs. The difference between the endo-skeletal and exo-skeletal portions of these elements of the plastron is as plain, and the contrast, indeed, is almost as great, in the young Tortoise as in the adult Trionyx, where the superadded ossification, at the expense of the dermal system, is characterized by the vermicular or punctate character of the exterior surface, a character common to the dermal ossified plates in the *Reptilia*, especially of the closely-allied Crocodilian order *.

The main purpose of the augmentation of the ordinary vertebral elements in the thoracic-abdominal region of the *Chelonia*, by the extension of ossification from them into the corium, and the consequent connation with those elements of dermal bony

* The distinction between the exo-skeletal and endo-skeletal parts of the plastron is so well-marked in the *Trionyx*, that the true explanation of the structure has forced itself, as it were, upon the authors who have given the most unqualified adhesion to the Cuvierian and Geoffroyian hypothesis. "Il est plus important de rappeler ici les caractères principaux—qui distinguent l'ordre des Tortues des trois groupes d'animaux rangés dans cette même classe des Reptiles; d'abord de tous les autres genres par la structure de leur squelette, dont les pièces qui constituent le tronc sont extérieures. Les vertèbres du dos, des lombes et du bassin étant soudées et solidement articulées, non seulement entre elles, mais avec les côtes et quelquefois le sternum, par de véritables sutures, ou unies par cette sorte d'engrenage que l'on nomme *synarthrose*; le tout forme ainsi une sorte de boîte,—une 'carapace'!—La partie inférieure du corps est également protégée par des pièces osseuses, correspondantes à un sternum, dont l'ensemble porte le nom de 'plastron.' "—Duméril and Bibron, Erpétologie Générale, 8vo, tom. i. p. 349, 1834.

The description of the carapace of a species of *Trionyx* is as follows:—"Cette espèce et la suivante sont les seules ou l'on ne compte sur le disque de la carapace que *sept callositées costales* de chaque côté d' l'épine dorsale, encore que ces deux espèces aient réellement huit paires de côtes comme tous les autres Gymnopodes. Cela vient de ce que chez le Gymnopode spinifère et chez le Gymnopode mutique il n'existe qu'une seule callosité pour les deux dernières côtes de chaque côte, tandis que dans les autres Gymnopodes les seize prolongemens costaux ont chacun leur callosité." The part here denominated 'callosity' is the connate dermal bone which is described in this memoir as the 'costal plate': but it is not more distinct in its mode of development, nor less connate with the subjacent rib in those *Trionyces*, which MM. Duméril and Bibron call 'Gymnopodes,' than it is in the ordinary Tortoises, Terrapenes and Turtles: only the superficial character of the superadded part is more distinct in the *Trionyces*: but it failed to draw the attention of the distinguished French erpetologists to a reconsideration of the homologies of the carapace which they had adopted.

plates, being the formation of a strong defensive abode, although the existence of the cuticular scutes, rather than of the parts of the endo-skeleton, determines the commencement of the ossification in the Tortoises, yet such ossification begins and proceeds in the dorsal and sternal integument of those *Chelonia*, e. g. *Trionyx* and *Sphargis*, that have no cuticular scutella, but a soft, uniform and lubricous integument. The influence, however, of this modification of the cuticular system on parts regarded as homologous with endo-skeletal elements in the ordinary *Chelonia*, is strikingly manifested, in the condition of the marginal plates and the variable proportions and even in the number of the ossified parts of the plastron, as *e. g.* in that of the *Trionyx granosus* (*Cryptopus*, D. & B.), in which a single dermal bony plate extends over the rudimentary hæmapophyses called hyosternals and hyposternals on each side. The cartilaginous matrix in the substance of the corium forming the margin of the carapace of *Sphargis* and *Trionyx*, receiving no stimulus from the presence of marginal scutella, is found to contain either mere scattered granules of ossific matter, as, *e. g.* in the *Trionyces* forming the genus *Gymnopus* of Dumeril and Bibron; or centres of ossification are established, as at the posterior part of the limb of the carapace in the species of *Cryptopus*, D. & B., which have no relation whatever with the presence, number or position of the vertebral ribs; and in these conditions of the border of the carapace we perceive a greater or less retention of the embryonic character noticed in the genus *Chelone*.

Summary.—The conclusions as to the homologies of the Chelonian carapace and plastron to which I have arrived from the observations above recorded and other details with which it has not been deemed necessary to encumber this communication, are as follow:—

1st. The centrum and the neural arch supporting the neural plate are parts the homologies of which admit of no question, and have given rise to none; but the neural plate itself is a dermal bone homologous with the median dermal scutes of the Crocodile's back-shield, but connate in some of the dorsal segments with the true neural spine in the *Chelonia*.

2nd. Only the free proximal and distal extremities of the costal plate and the narrow smooth prominent tract * continued from the one end to the other along the under part of the plate, represent the 'pleurapophysis' or vertebral rib; and this rib is accordingly simple, as in other reptiles with a tripartite heart: the external expanded portion which joins the neural plate is a dermal bone homologous with the medio-lateral dermal scutes in the Crocodiles, but connate with the pleurapophysis in the *Chelonia*.

3rd. The marginal plates are wholly dermal scutes; and even on the hypothesis that any of them, such for example as are penetrated by the free ends of the pleurapophyses, belong to the endo-skeleton, yet these answer rather to the accessory in-

* This part is well shown in the view of the inner surface of the carapace of the 'Water-Tortoise,' which Cheselden gives in the beautiful plate facing the 3rd Chapter of his magnificent 'Osteographia,' fol. 1733.

tervening pieces between the pleurapophyses and hæmapophyses of the Crocodilian thorax*, than to the hæmapophyses in their totality.

4th. The parial or lateral parts of the plastron, more especially the hyosternals and hyposternals, are the true 'hæmapophyses'; but in connation with dermal bony plates to which their characteristic breadth, especially in the land and freshwater Chelonians, is chiefly due. The entosternal, and perhaps the episternals, which repeat the transverse bar of the T-shaped sternum in *Lacertia* and *Monotremata*, are the sole parts of the plastron which can be referred to the 'sternum' in special homology and to the 'hæmal spine' of the typical vertebra in general homology.

Supplement.

The justly-merited reputation of Prof. Rathke as an embryologist, and the fact of his having deduced his views of the mixed nature of the thoracic-abdominal part of the skeleton of the Chelonian Reptiles from observation of its development, equally demand that his conclusions should not be abandoned without special grounds being assigned. Rathke concludes, as has been before stated, that the carapace belongs to the endo-skeleton exclusively†, and the plastron as exclusively to the exo-skeleton‡.

With regard to the carapace, he says, "The spinous processes are already developed from the second to the eighth dorsal vertebræ before the exclusion of the embryo, ... they remain pretty short, but contrary to the general laws of development of the vertebrate animals, they grow so much in breadth, that they form, after their ossification, a series of horizontal plates of moderate size§." He also takes occasion to confute the assertions of Carus, Wagner and Peters, that these plates are first developed independently in the derm and afterwards coalesce with the spines of the subjacent vertebræ. My observations concur with those of Rathke in regard to the fact that the neural plates, answering to the eight vertebræ of the carapace, are not developed independently of the neural spines, but are connate with, or ossified continuously from them‖. Nevertheless the position of the pre-existing fibro-cartilaginous matrix, and the distinctive character of the resulting ossification, appear to me to be stronger grounds for determining their dermal homology, than the mere fact of their connation in opposition to that view. The radius and ulna of the Frog are not only confluent but connate; *i. e.* they are progressively or continuously ossified from a

* These are well shown by Cheselden in the side view of the skeleton of the Crocodile, which forms the vignette of chapter iii., *op. cit.* They are not noticed in either of the editions of Cuvier's 'Ossemens Fossiles,' or of the 'Leçons d'Anatomie Comparée,' and are therefore unnoticed in most of our English compilations of Comparative Anatomy.

† Ueber die Entwickelung der Schildkröten. 4to, p. 105.

‡ Ib. p. 122–129.

§ *Loc. cit.*, and Annales des Sciences Naturelles, Mars, 1846.

‖ At least in the *Testudo* and *Chelone*. In some *Trionyces* ossification extends into the eighth neural plate from the median ends of the eighth costal plates, and in a new species which I have called *Trionyx planus* the same modification supersedes the seventh neural plate. These varieties are very significative of the dermal character of the neural plates.

common centre, yet their essential homologies are neither thereby destroyed nor much masked.

The unimportant, one might almost say accidental character of connation, in regard to the neural plates of the carapace, is shown by its absence in at least one-fourth of the series of those plates. Rathke admits that the first or nuchal plate, the ninth, tenth, eleventh and twelfth of the median series of plates of the carapace are developed from independent centres in the substance of the corium, and are therefore dermal bones. Now it is indisputable that these are the homotypes or serial homologues of the second to the eighth of the same median series of plates. The mere circumstance of connation of these plates with the closely subjacent vertebræ cannot make so essential a difference as is implied by their classification in a distinct skeleton-system from that to which their homotypes are admitted to belong.

With regard to the 'costal plates,' M. Rathke, after rightly stating that "all, or nearly all, of the ribs of the trunk-vertebræ are cylindrical until the exclusion of the embryo," proceeds to say, "they then begin to increase in breadth; ..... this increase commences at the place where the neck of the rib joins the body of the rib, and thence advances more or less towards the (distal) extremity: it becomes so considerable, that the bodies of all the ribs, by reason of the complete absence of intercostal muscles, come into contact on each side, either through their entire length, as in the genera *Emys*, *Terrapene*, *Testudo*, *Trionyx*, or nearly their whole length, as in *Chelone**."

The author appears to have traced, with great industry and perseverance, the development of the carapace in each of the genera which he cites in the above quotation: but the very general terms in which such development is described might have been suggested by a mere comparison of its results as they are manifested in the adult carapaces, except that in no species of *Trionyx* are the ribs united throughout their entire length: the extremity of the actual rib projects from the peripheral end of the superincumbent costal plate, even in the oldest specimens. M. Rathke proceeds:— "Soon after the eight pairs of ribs have begun to expand a process is sent off from above near the spinal column, which by its growth overlaps the few and slender dorsal muscles, and unites with the spinous process of the vertebræ†." Such a description of the development of the costal plates could be suggested, I believe, only by observation of a tolerably young specimen of *Chelone* or *Emys*. There is no mention of the development of the costal plates in the Tortoise (*Testudo*) by superposition of osseous matter upon the rib, the supporting part of which rib retains its normal form without expanding: there is no allusion to the alternately varying position of the superimposed dermal ossification in regard to the rib supporting it, nor to the relation of the incipient costal plates to the angles of union of the epidermal scutes. Perhaps these facts, so important in guiding us to the right homology of the costal plates of the carapace, were manifested in the young Tortoises examined by Prof. Rathke, though he has not described them: and yet it would be unfair, without

* *Loc. cit.* † *Loc. cit.*

stronger evidence, to suppose such defects in his description. They are, however, plainly demonstrated in my preparations, and are accurately represented in the figures 4 and 5 of Plate XIII. I entirely concur with Prof. RATHKE in regarding the marginal plates as dermal bones: in every particular of developmental character they agree with one-fourth of the median series of bony plates of the carapace (neural plates); and in every respect, save connation with endo-skeletal bones, they agree with the rest of the median series and with all the costal series of bony plates of the carapace.

Finally, there remains for consideration Prof. RATHKE's peculiar hypothesis of the nature of the plastron.

"The development of the plastron," he says, "takes place later than in Birds and Mammals: the cartilaginous basis consists of two pairs of very narrow and thin cartilages, one in front and the other behind the umbilical aperture: there is likewise formed a fifth azygous piece in most *Chelonians*" (he excepts *Sphargis* with a doubt), "between the two anterior parial pieces.... Subsequently there are developed in these different cartilages, more numerous osseous pieces, ordinarily, or perhaps always, nine in number. Their respective size varies greatly, according to the different species of Chelonians; for either they grow in such a way, the one in front of the other, that they meet by their corresponding borders in their whole length, so as to constitute a continuous plastron, or their growth is more restricted, and then they form a plastron open in the middle; or they constitute merely a narrow ring, as is probably the case in the *Sphargis**."

He alludes to other modifications of growth, which might equally have been suggested by the known varieties of the plastron in the adults of the different genera and species of *Chelonia*; *e.g.* where it extends forwards beyond the neck, and backwards beyond the tail, which he thinks may probably depend upon the presence of an inferior fold of chorion existing in front of the fore-feet, and of another inferior fold behind the hind-feet: although he admits that where, as in the *Trionyx*, such folds occur, they are not occupied by the plastron, which fact invalidates the hypothesis.

My observations do not agree with those of RATHKE, which have led him to ascribe the eight parial pieces of the plastron to the development of as numerous osseous pieces in the two pairs of primitive slender cartilages. I find no other ossification set up on the anterior pair of those cartilages than that which results in the formation of the hyosternals; and no other in the posterior pair than that which results in the formation of the hyposternals. The episternals unquestionably have independent cartilages, and so I believe have the xiphisternals, though I have failed to get so clear a demonstration of the latter.

The primitive cartilages of the true sternum (entosternal) and the thoracic-abdominal hæmapophyses (hyosternals and hyposternals) are distinct from, and deeper-seated than, the thin stratum of cartilage-cells which pervades and thickens the ventral fibrous integument. I am unwilling to suppose that RATHKE could have ever wit-

* *Loc. cit.*

nessed the marked distinction between the ossification of these endo-skeletal parts and the superadded dermal ossified layer, and have made no mention of it. He, in fact, maintains his opinion, "that the plastron is nothing else but a part of the dermo-skeleton, and that it has nothing in common, in an anatomical point of view, with the sternum of other animals*," thus diverging to an opposite extreme from that of the Geoffroyan hypothesis, although rather by arguments drawn from the relative position of other parts of the skeleton and from Comparative Anatomy than from the actual phenomena of the development of the plastron.

"If the plastron of the Chelonia were the homologue of the sternum in other Vertebrates," says RATHKE, "one must also admit that the bones composing the shoulder and pelvis are situated in a manner entirely contrary to the general disposition of those parts in other animals." But that remark would equally apply as an argument against the carapace being homologous with the vertebræ and ribs, as RATHKE contends it to be. It appears to me, however, that the peculiarly advanced position of the scapular arch in the embryo Chelonia, and, at its first appearance in all other Vertebrates, in relation to the thoracic hæmal arches,—a transitory relative position so beautifully explained by the recognition of the scapular arch as the hæmal arch of the occipital vertebra—equally explains and removes the anomaly of its position in regard to the plastron of the adult Chelonians as in regard to the carapace. In both instances the Chelonian peculiarity or anomaly, in the relative position of the bones of the shoulder, is due to the retrogradation of the scapular arch and the concomitant expansion of certain succeeding hæmal arches; as, for example, that formed by the second pair of dorsal ribs above, and by the episternal and hyosternal bones below; the one extending above the arch as a roof, the other beneath it as a floor. The discordance of the relations of the scapular and pelvic arches of the Chelonians with those in other Vertebrates no more necessitates the assumption that all the plastron belongs to the dermo-skeleton, than that all the carapace does.

With regard, indeed, to the relations of the pelvis to the plastron, whilst we should look amongst other Vertebrates, in vain, for instances in which the ossified exo-skeleton is developed beneath it, as RATHKE supposes it to be in the *Chelonia* (fig. 8, in which *ps* and *xs* are referred by that author to the exo-skeleton†), we have not far

* *Loc. cit.*

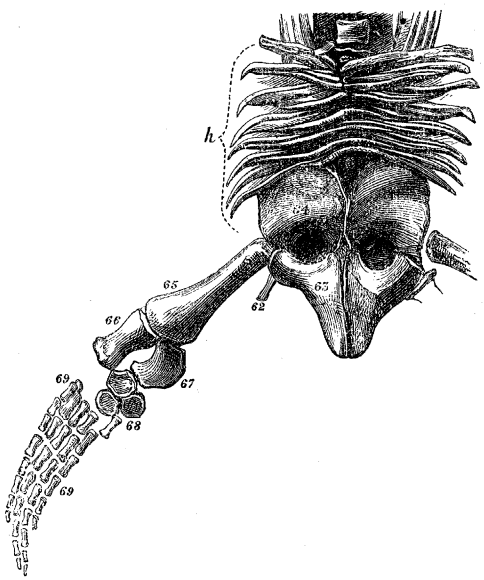
† In the figures 8 and 9 *hh* are the hæmapophyses or abdominal ribs, specified in the *Chelonia* as *hs* hyosternals, *ps* hyposternals, and *xs* xiphisternals: 62 is the modified pleurapophysis called 'ilium'; 63 and 64, the modified hæmapophyses, called respectively 'ischium' and 'pubis'; 65, femur; 66, tibia; 67, fibula; 68, tarsus; 69, metatarsus and phalanges.

In a fossil *Emys* from Sheppey, described by Professor BELL, Sec.R.S., in our joint Monograph on the Fossil Chelonia of the London Clay, an intercalated piece is wedged in between the outer part of the interspace of the hyosternal and hyposternal on each side, like the dismemberments of the abdominal ribs at the outer part of that group of bones in the *Plesiosaurus*: and in another fossil Emydian from the same formation and locality, an intercalated bony piece extends across between the hyosternal and hyposternal on each side of the plastron. See Description of *Platemys Bullockii*, in my Report on British Fossil Reptiles, Report of the British Association, 1841, p. 164.

to seek for examples in which ordinary elements of the endo-skeleton are extended between the pelvis and the ventral integuments. Not to speak of the *Plesiosaurus* (fig. 7), in which the underlapping of the pubic-bones 64, by the abdominal ribs (*h*), might be due to displacement of the fossilized parts; the Puffins (*Fratercula*), the Guillemots (*Uria*) (fig. 9), and other common sea-birds of our coasts give the examples of the sternum prolonged backwards to beyond the vertical line traversing the acetabulum; whilst the hæmapophyses (*h*, *h*, ossified cartilages) of the three or four posterior ribs extend backwards beyond or as far as the most backwardly prolonged parts of the pelvis (63, 64), exactly in the relative position which the xiphisternals and hyposternals bear to the pelvis of the *Chelonia*.

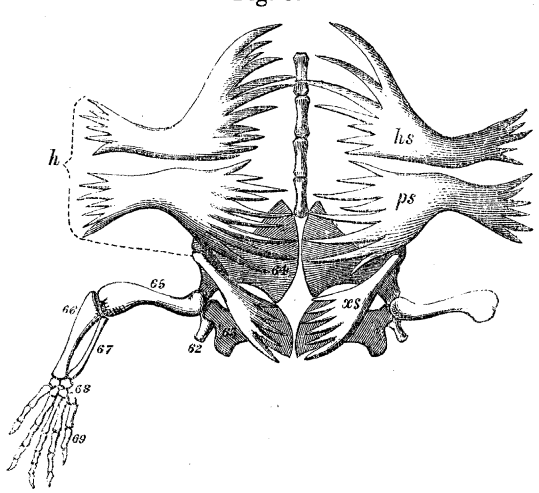
In this comparison it is interesting also to discern the harmony which pervades the same vertebral elements in the characteristic forms which they assume in the same species. In the sea-birds cited the ossa pubis (64), or the hæmapophyses of the pelvic arch, are long and slender, like the costal hæmapophyses (*h*) beneath them: in the Chelonian reptiles the ossa pubis (64) are broad and expanded, like the costal hæmapophyses (*ps*, *xs*), which equally intervene between them and the ventral integument. Nature is ever liberal in rewarding with the perception of such harmonies whoever patiently investigates and rightly comprehends her arrangements.

Fig. 7.



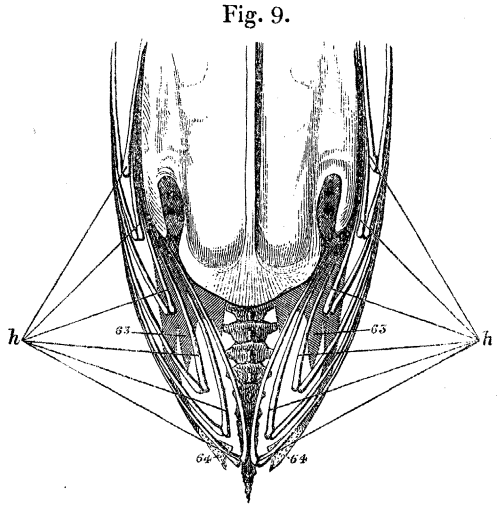
Relations of thoracic to pelvic hæmapophyses, Plesiosaurus.

Fig. 8.



Relations of thoracic to pelvic hæmapophyses, Chelonian.

Fig. 9.



Relations of thoracic to pelvic hæmapophyses, Bird (*Uria Troile*).

Fig. 1a.

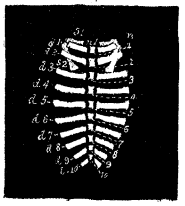


Fig. 1.

Fig. 3.

Fig. 2.

Fig. 2a.

Fig. 3a.

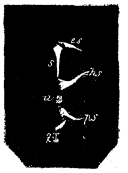


Fig. 6.

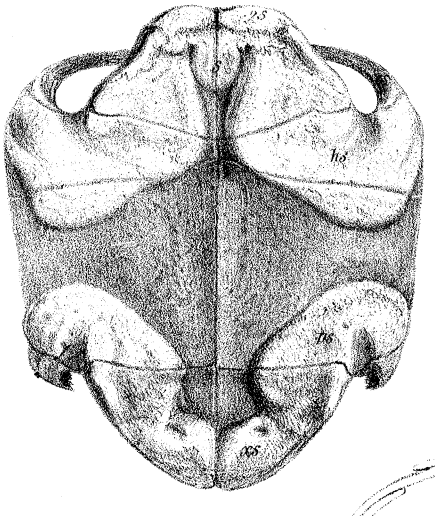


Fig. 7.

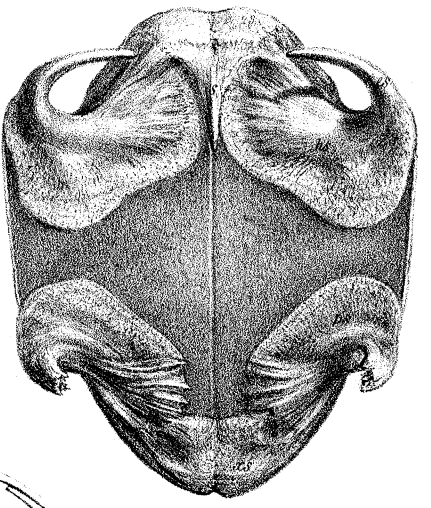


Fig. 8.

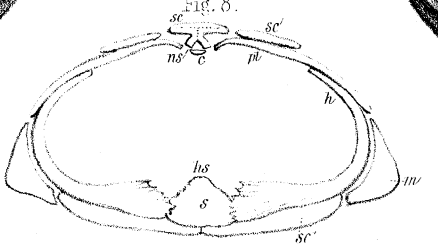


Fig. 4.

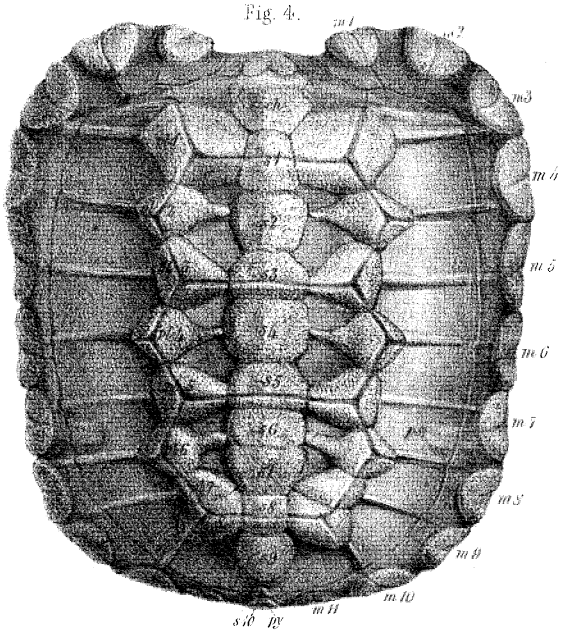
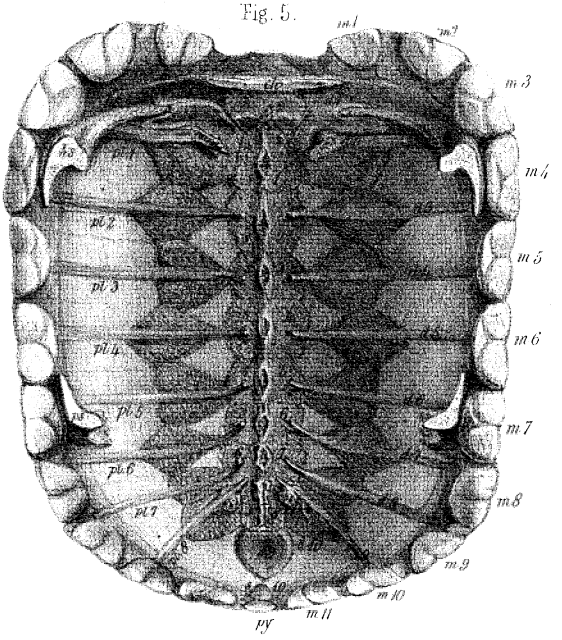


Fig. 5.



Description of the Plate.

PLATE XIII.

(All the figures are of the natural size.)

Fig. 1. Embryo Turtle (*Chelone Mydas*).
1 *a*. Ossified parts of its carapace.
Fig. 2. Side view of the same embryo.
2 *a*. Side view of the ossified parts of its carapace.
Fig. 3. Front view of the same embryo.
3 *a*. Ossified rudiments of the plastron.
Fig. 4. External surface of the incipient carapace of a young Tortoise (*Testudo indica*).
Fig. 5. Internal view of the same carapace.
Fig. 6. External surface of the plastron of the same young Tortoise.
Fig. 7. Internal view of the same plastron.
Fig. 8. Ideal section of the same carapace and plastron.
The letters and figures are explained in the text.